# PARTIAL PHOTOPERIODIC CONTROL OF DIAPAUSE IN THREE POPULATIONS OF THE FRESHWATER COPEPOD *DIAPTOMUS SANGUINEUS*

NELSON G. HAIRSTON, JR.[1] AND EMILY J. OLDS[2]

*[1]Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853; and [2]Entomology Department, Michigan State University, East Lansing, Michigan 48824*

## ABSTRACT

Populations of the freshwater calanoid copepod *Diaptomus sanguineus* inhabiting three Rhode Island ponds switch from making subitaneous (immediately hatching) to diapausing eggs on different dates. From results of previous research the timing of diapause appears to correspond closely to the individual causes of seasonally harsh conditions in each pond. The results of rearing copepods from each pond in controlled laboratory environments indicate that each population possesses a unique spectrum of sensitivity to photoperiod. The responses obtained, however, fail to describe adequately either the rapidity with which the onset of diapause occurs in natural populations, or the differences in diapause timing between ponds. In initiating diapause, the copepods must respond to seasonal environmental cues other than critical photoperiod.

## INTRODUCTION

Diapause is a physiological and developmental response adopted by a broad variety of animals as a means of avoiding seasonally uninhabitable periods in the environment. Annual climatic changes are frequently responsible for the onset of harsh conditions, and examples of temperate zone animals that enter diapause prior to winter are especially well documented (see Danilevskii, 1965; Beck, 1980; and Tauber *et al.*, 1985 for reviews). When a species' geographical range covers a broad spectrum of latitudes, intolerable winter conditions for local populations may begin at markedly different times of year. Often these populations exhibit responses to diapause-controlling cues correlated with the climatic gradient. For example, animals collected at northern latitudes initiate diapause earlier in the autumn or at longer photoperiods than those collected further south (*e.g.*, Showers *et al.*, 1975; Holtzer *et al.*, 1976; Lumme and Oikarinen, 1977; Marcus, 1984). Several investigators have shown that such variation is genetically based indicating that populations are specifically adapted to the latitudes at which they reside (Masaki, 1963, 1967; Showers *et al.*, 1975; Istock, 1981; Marcus, 1984). At the same time, there is evidence that some local populations retain additive genetic variance for diapause traits (Hoy, 1977; Istock, 1981; Lumme, 1982; Hairston and Walton, 1986), presumably maintained by local variation in selection pressures.

A third potential source of variation in diapause is that between populations residing at the same latitude. For such variation to exist, however, local habitats must be sufficiently isolated or represent sufficiently different selective regimes to overcome the homogenizing force of dispersal. The planktonic freshwater copepod *Diaptomus sanguineus* is a resident of small lakes and ponds in northeastern North America

(Wilson, 1959). Within any given geographical area, many of these bodies of water differ in potentially important ways such as basin depth with its accompanying effect on the annual water-temperature cycle, seasonal permanency, and the types of planktivores present.

Three populations of *D. sanguineus* residing in three ponds in southern Rhode Island exhibit distinct seasonal patterns of egg diapause (Fig. 1A). In Bullhead Pond the copepods switch from production of subitaneous (immediately hatching) eggs to production of diapausing eggs in late March; in Pond C diapause is initiated at the end of April, and in Pond A diapause begins principally in mid-May (Hairston and Munns, 1984; Hairston *et al.*, 1985; Hairston, 1986). These patterns are regularly repeated in successive years and represent real differences between reproductive phenologies of the three populations even though the ponds in which they live are geographically quite close to each other (Ponds A and C are <200 m apart and *ca.* 27 km from Bullhead Pond). We showed previously (Hairston and Olds, 1984) that female copepods reciprocally transplanted between Bullhead Pond and Pond A began production of diapausing eggs at the time of year appropriate to their home pond rather than the pond to which they were transferred, and concluded that *D. sanguineus* was physiologically unable to alter its reproduction in response to changes in pond type. What then is the basis for the differences in timing of diapause observed between ponds?

One obvious possibility is that the copepods have distinct adaptations suitable to the local habitat in which they live. Hairston and Munns (1984) showed that *D. sanguineus* in Bullhead Pond began production of diapausing eggs at the appropriate time to avoid a spring increase in planktivory by resident sunfish. Ponds A and C, on the other hand, are temporary bodies of water and contain no fish. In Pond C the copepods switch to making diapausing eggs at the correct time of year to avoid seasonally intense predation by the dipteran larvae *Chaoborus* and *Mochlonyx* (Hairston *et al.*, 1985; Hairston, 1986). Neither of these predatory flies is abundant in Pond A, where *D. sanguineus* appears to produce diapausing eggs as an adaptation to survive periods of pond drying (Hairston *et al.*, 1985; Hairston and Olds, in prep.). If timing of diapause is a distinct adaptation of the copepods to the separate conditions found in each pond, then the differing seasonal patterns of reproduction must have a genetic basis. Photoperiod is the environmental cue initiating diapause in a broad variety of animals including insects (*e.g.*, Beck, 1980; Tauber and Tauber, 1981), mammals (Flint *et al.*, 1981), and crustacean zooplankton (Einsle, 1964; Stross and Hill, 1965; Stross, 1969; Spindler, 1971; Watson and Smallman, 1971; Marcus, 1980). As a result, it is logical to ask if the different *D. sanguineus* populations switch from production of subitateous eggs to diapausing eggs at different critical day lengths.

The data in Figure 1A can be replotted as the fraction of each population carrying subitaneous eggs (as opposed to diapausing eggs) at the day length prevailing when the copepods were collected (Fig. 1B). If the interpopulation differences in the timing of diapause initiation result from the copepods being sensitive to different critical day lengths, then animals collected at each of the three ponds and reared in the laboratory under a series of appropriately chosen photoperiods should respond with distinct patterns of subitaneous and diapausing egg production. Specifically, at day lengths shorter than about 11 hours all copepods should make subitaneous eggs, at intermediate day lengths of around 13 hours Bullhead Pond copepods should make diapausing eggs while copepods from Ponds A and C should make subitaneous eggs, and at day lengths longer than about 14.5 hours all copepods should make diapausing eggs. Here we test this hypothesis as a route to understanding the causes underlying the distinct reproductive phenologies of *D. sanguineus* living in Bullhead Pond, Pond A, and Pond C.
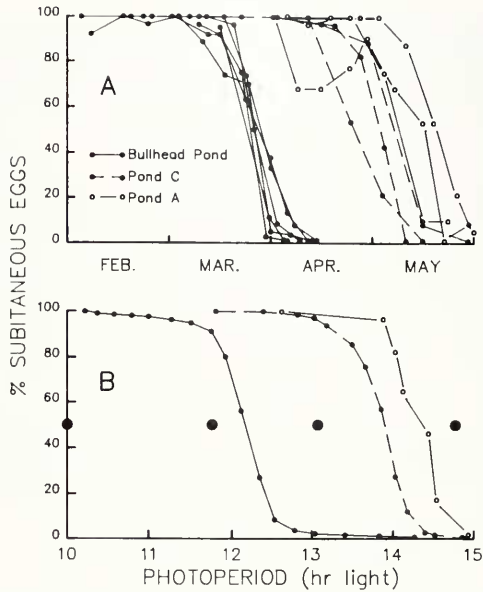
FIGURE 1. The fractions of female *Diaptomus sanguineus* from three Rhode Island ponds making subitaneous (immediately hatching) eggs, as opposed to diapausing eggs, as a function of time of year. A. Egg type *versus* date of collection. The lines are summaries of data from Hairston and Munns (1984), Hairston *et al.* (1985), and Hairston (1986) showing the annual variation in timing of diapause. Data points after the switch to production of diapausing eggs are omitted here to facilitate illustration. Copepods in temporary Pond A have been shown in some years to return to production of subitaneous eggs for brief periods in June after the pond refilled with water from heavy rains. These reversals, discussed in detail elsewhere (Hairston and Olds, 1984; in prep.), have been omitted here to simplify illustration. B. Egg type versus prevailing day length (sunrise to sunset) on the date of collection. Photoperiodic responses are calculated from mean fractions of females making subitaneous eggs for the years illustrated in A. Closed circles denote photoperiods tested in laboratory experiments.

## MATERIALS AND METHODS

The study sites, Bullhead Pond and Ponds A and C, are described in detail elsewhere (Hairston, 1980; Hairston *et al.*, 1983; Hairston and Olds, 1984). *Diaptomus sanguineus* has 12 separate instars: six naupliar and six copepodid stages, plus an egg stage which the female copepods carry in a sac attached to their urosome. The animals are active in the water column during winter and spring, and make two or three generations per year before producing diapausing eggs (Hairston and Olds, 1984; Hairston *et al.*, 1985). Live first and second stage nauplii were collected during March through May from each of the three Rhode Island ponds using a 75 $\mu$m mesh net. The nauplii were isolated in 2 L glass jars filled with 1 L of filtered pond water; 200 nauplii per jar. These cultures were fed twice weekly from algal stocks, and maintained with approximately $1 \times 10^7$ cells $\cdot$ ml$^{-1}$ of *Chlamydomonas* sp. and $1 \times 10^5$ cells $\cdot$ ml$^{-1}$ of *Euglena* sp. The copepods were reared at 9°C and at a series of photoperiods in controlled environment chambers. Survival under these laboratory conditions was 40% to 60% from nauplius to adult. Raising the animals from early naupliar instars ensured more than sufficient time for the copepods to respond to the photoperiod treatments. Elsewhere we have shown that upon exposure to a change of day length, female *D. sanguineus* can alter the type of egg they produce within three clutches (Hairston and

Olds, in prep.). Thus, unlike many species of insects (Beck, 1980), there is no early sensitive instar that irreversibly programs the copepod's diapause phenology. It seems likely that egg type in *D. sanguineus* is determined principally by females because diapausing eggs have a thick, highly structured chorion laid down by the mother whereas subitaneous eggs have a thin homogeneous chorion, and because the two egg types are provisioned differently (Hairston and Olds, 1984). Probably due to these structural differences and the physiological adjustments they imply, clutches are composed of either subitaneous or diapausing eggs. Mixed clutches are never made. Females do not store sperm and mating is required before each clutch can be produced. We do not know, however, what role, if any, males play in determining egg type.

The photoperiods were chosen to conform with the design described in the Introduction (Fig. 1B). Day length 9:55 corresponds to the date 25 January (sunrise to sunset), well before the switch to diapause in any of the populations. Day length 13:05 corresponds to 10 April when the Bullhead Pond population has almost completely shifted to making diapausing eggs but the Ponds A and C populations still produce principally subitaneous eggs, and 14:45 corresponds to 28 May when all populations produce mainly diapausing eggs. Bullhead Pond copepods also were reared at a fourth daylength, 11:40 corresponding to 10 March shortly before they switch from subitaneous to diapausing eggs.

The copepods were allowed to mature in the 2 L jars. Females carrying their first clutches were isolated individually in 15 ml of medium in 6-well tissue culture plates, and observed until either their eggs had hatched or they had dropped their egg sacs. The females were then placed in new 2 L jars with males and allowed to produce a second clutch. Copepods carrying their second egg clutches were reisolated in the tissue culture wells and egg hatching was again monitored. The process was continued until all females had produced three clutches. Females were pooled in 2 L jars because mating success was substantially higher in this arrangement than when males and females were isolated in small volumes of water. The procedure, however, does not permit a determination of the sequence of clutches made by individual females. Subitaneous and diapausing eggs cannot be distinguished under light microscopy, but we have shown previously (Hairston and Olds, 1984; Hairston and Munns, 1984) that in contrast to diapausing eggs, subitaneous eggs hatch rapidly, usually within one week after being laid. As in our earlier research, eggs that hatched within two weeks after production were designated subitaneous eggs, whereas those that had not hatched during this period were designated diapausing eggs. By these methods we established the fractions of subitaneous and diapausing eggs made by *D. sanguineus* from each of the three ponds when reared under the three or four experimental photoperiods. In addition, the fractions of egg types produced as first, second, and third clutches were determined independently in each treatment.

## RESULTS

Populations of *Diaptomus sanguineus* from the three ponds have distinct photoperiodic responses (Fig. 2). In each case, copepods reared under short day lengths produced significantly greater fractions of subitaneous clutches than those reared under longer photoperiods (Ponds A and C, $\chi^2 = 116.2$ and $94.9$ respectively, df $= 2$, $P \ll .001$; Bullhead Pond, $\chi^2 = 211.1$, df $= 3$, $P \ll .001$). Figure 2 illustrates both the results from the treatments described here, and those from a second experiment in which Bullhead Pond and Pond A copepods reared under winter conditions (8L:16D, $4 \pm 1°C$) produced only subitaneous eggs and those reared under summer conditions (16L:8D, $20 \pm 1°C$) made only diapausing eggs (Hairston and Olds, in prep.).
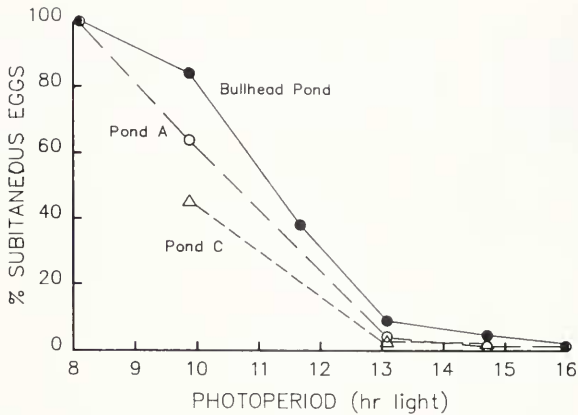
FIGURE 2. The fractions of subitaneous (immediately hatching) clutches of eggs produced by female *Diaptomus sanguineus* reared at the photoperiods illustrated. Data are for all clutches regardless of order of production. For sequence of clutch production see Table I. Experiments at intermediate day lengths were run at $9 \pm 1°C$, whereas those at 8L:16D and 16L:8D were run at $4 \pm 1°C$ and $20 \pm 1°C$ respectively.

The levels of response differed significantly among *D. sanguineus* drawn from different ponds. At day length 9:55 hours Bullhead Pond females made a greater fraction of subitaneous eggs than either Pond A or Pond C females ($\chi^2 = 14.67$ and 41.68 respectively, df = 1, $P < .001$), and Pond A females made a greater fraction of subitaneous eggs than Pond C females ($\chi^2 = 6.37$, df = 1, $P < .02$). At longer photoperiods where subitaneous egg production was generally low, Bullhead Pond results differed significantly from Pond C at day length 13:05 hours ($\chi^2 = 5.44$, df = 1, $P < .02$), and from Pond A at day length 14:45 hours ($\chi^2 = 3.91$, df = 1, $P < .05$).

Although others have found that diaptomid copepods tend to switch from making subitaneous eggs to diapausing eggs as they grow older (Roen, 1957; Champeau, 1970; Gehrs and Martin, 1974; Walton, 1985), and such a reproductive pattern is expected theoretically in highly variable environments (Hairston *et al.*, 1985; Hairston and Olds, in prep.), no clear trend of this sort is present in our results (Table I). Under a photoperiod of 9:55L both Pond A and Pond C females reduced the fraction of subitaneous eggs they produced in second compared to first clutches ($\chi^2 = 6.61$ and 7.89 respectively, df = 1, $P < .02$), but in each case they returned to making more subitaneous eggs in their third clutches than in their second clutches.

## DISCUSSION

Our hypothesis was that the distinct reproductive phenologies of *Diaptomus sanguineus* living in three Rhode Island ponds (Fig. 1A) reflect unique adaptations to the seasonal events in those habitats. Specifically we proposed that copepods taken from different populations begin production of diapausing eggs at different times of year because they respond proximately to different photoperiods. In a broad sense the hypothesis is born out (Fig. 2), in that (1) the copepods make principally subitaneous eggs at short photoperiods and principally diapausing eggs at long photoperiods and (2) significant differences in this response pattern exist between populations. However, the change from subitaneous (nondiapausing) eggs to diapausing eggs occurs more gradually and over a much wider range of photoperiods than is consistent with the field data (*cf.*, Fig. 2 and Fig. 1B). Furthermore, the specific photoperiods at which

TABLE 1

*Fractions of subitaneous (immediately hatching) clutches of eggs as opposed to diapausing clutches, produced by female* Diaptomus sanguineus *reared at four photoperiods, and the change in this fraction as the females aged (i.e. 1st, 2nd, and 3rd clutches)*

| Photoperiod | Clutch sequence | Pond | | |
|---|---|---|---|---|
| | | Bullhead | A | C |
| 9:55L–14:05D | 1st | 0.85 (72)[1] | 0.62 (69) | 0.53 (53) |
| | 2nd | 0.82 (50) | 0.42 (24) | 0.22 (32) |
| | 3rd | 0.90 (20) | 0.50 (4) | 0.78 (9) |
| 11:40L–12:20D | 1st | 0.38 (131) | | |
| | 2nd | 0.36 (75) | | |
| | 3rd | 0.50 (2) | | |
| 13:05L–10:55D | 1st | 0.14 (98) | 0 (55) | 0.03 (72) |
| | 2nd | 0 (47) | 0 (43) | 0 (41) |
| | 3rd | 0 (6) | 0.21 (24) | 0.10 (10) |
| 14:45L–9:15D | 1st | 0.04 (48) | 0 (70) | 0.02 (58) |
| | 2nd | 0 (9) | 0 (28) | 0.03 (32) |
| | 3rd | — (0) | 0 (12) | 0 (5) |

[1] The values in parentheses give the total numbers of reproducing females in each treatment.

the switches take place in the field populations differ markedly from those recorded in the laboratory.

Female copepods collected from Bullhead Pond carry principally subitaneous eggs until mid-March when day length exceeds 11.5 hours. The switch in egg types then occurs rapidly and by the end of March, at day lengths of 12.5 hours, nearly all have switched to making diapausing eggs (Fig. 1). In contrast, Bullhead Pond copepods cultured in the laboratory make a small, but significant, fraction of diapausing eggs when exposed to only about 10 hours of light (comparable to the day length on 25 January), and yet continue to make a significant fraction of subitaneous eggs at a photoperiod greater than 13 hours of light (comparable to the day length on 10 April). Half of the females in the field have switched to carrying diapausing eggs at a day length of 12.2 hours (or 24 March), whereas in the laboratory this point is reached much earlier at exposure to about 11.2 hours of light (comparable to 27 February). For Ponds A and C, the differences between the populations in nature and their behavior in the laboratory are even more striking. One half of the female copepods in Pond A have switched to making diapausing eggs when day length has reached about 14.3 hours (14 May), but in the laboratory 50% diapause lies at 10.6 hours of light (comparable to 12 March). In Pond C, one half of the females have switched to diapause at a day length of 13.9 hours (29 April), whereas in the laboratory 50% diapause occurs at less than 9.9 hours of day light (comparable to 25 January).

Not only do laboratory-reared *D. sanguineus* exhibit photoperiod responses inconsistent in timing with the patterns of reproduction recorded in the field, but the order of the responses is also incongruous (*cf.* Fig. 1B and Fig. 2). In the natural populations, Bullhead Pond females are the first to switch to producing diapausing eggs, followed by Pond C females, and finally by those in Pond A. In the laboratory, however, Pond C copepods switch to diapause at the shortest day lengths followed by Pond A and Bullhead Pond copepods. The fact that the differences in laboratory photoperiod responses between the three populations are statistically significant (Re-

sults) indicates that the dissimilarities are inherent. Since all the copepods were cultured under identical laboratory conditions, environmental sources of variation were presumably removed, and the populations from the three ponds apparently differ genetically.

It is clear that the natural populations of *D. sanguineus* must use environmental cues other than critical photoperiod to set the timing of diapause. The behavior observed in the laboratory, although real, represents only a single component of a more complex response pattern. Without further experimentation it is difficult to say what factors might be involved in a complete characterization of the environmental cue for the onset of diapause. The photoperiodic response of many animals is modifiable to some extent by temperature (*e.g.*, Beck, 1980), including the marine calanoid copepod *Labidocera aestiva* studied by Marcus (1982). As spring progresses into summer, *D. sanguineus* experiences both an increase in day length and an increase in water temperature, and one might suppose that each population is adapted to respond to a unique combination of these two environmental variables. Two difficulties with such a suggestion are (1) that exposing Pond A and C animals to a temperature abnormally low for the photoperiod used should have enhanced the production of subitaneous over diapausing eggs, but instead had the opposite effect, and (2) that even the appropriate temperature and photoperiod combination did not produce the correct response by Bullhead Pond copepods. A third type of environmental information available to the copepods at all three ponds is the direction and rate of change of photoperiod. Tauber and Tauber (1970) have shown for a lacewing (Neuroptera) that autumnal diapause can be induced at relatively long photoperiods if the insects are exposed to decreasing rather than constant day lengths. Sensitivity to such a change in day length, were it to exist in *D. sanguineus*, could explain both the rapidity and the timing of the onset of diapause. Whatever the environmental cue or cues used by the copepods to time the switch to diapause, discovering their precise nature will permit more detailed investigation of the evolutionary bases of interpopulation differences in reproductive phenology.

## LITERATURE CITED

BECK, S. 1980. *Insect Photoperiodism.* Academic Press, New York. 387 pp.

CHAMPEAU, A. 1970. Étude de la vie latent chez les Calanoides (Copépodes) caractéristiques des eaux temporaires de Basse-Provence. *Ann. Fac. Sci. Marseille* **44**: 155–189.

DANILEVSKII, A. 1965. *Photoperiodism and Seasonal Development of Insects.* Oliver and Boyd, Edinburgh. 283 pp.

EINSLE, U. 1964. Larvalentwicklung von Cyclopoiden unter Photoperiodik. *Naturwissenschaften* **51**: 345.

FLINT, A. P. F., M. B. RENFREE, AND B. J. WEIR. 1981. Embryonic diapause in mammals. *J. Reprod. Fertil. Suppl.* **29**. 260 pp.

GEHRS, C., AND B. D. MARTIN. 1974. Production of resting eggs by *Diaptomus clavipes* Schacht (Copepoda: Calanoida). *Am. Midl. Natl.* **91**: 486–488.

HAIRSTON, N. G., JR. 1980. On the diel variation of copepod pigmentation. *Limnol. Oceanogr.* **25**: 742–747.

HAIRSTON, N. G., JR. 1986. Diapause as a predator avoidance adaptation. in *Predation: Direct and Indirect Impacts on Aquatic Communities,* W. C. Kerfoot and A. Sih, eds. Univ. Press of New England, Hanover. (In press.)

HAIRSTON, N. G., JR., AND E. J. OLDS. 1984. Population differences in the timing of diapause: adaptation in a spatially heterogeneous environment. *Oecologia* **61:** 42–48.

HAIRSTON, N. G., JR., AND W. E. WALTON. 1986. Rapid evolution of a life history trait. *Proc. Natl. Acad. Sci.* **83:** 4831–4833.

HAIRSTON, N. G., JR., AND W. R. MUNNS, JR. 1984. The timing of copepod diapause as an evolutionarily stable strategy. *Am. Nat.* **123:** 733–751.

HAIRSTON, N. G., JR., E. J. OLDS, AND W. R. MUNNS, JR. 1985. Bet-hedging and environmentally cued strategies of diaptomid copepods. *Int. Ver. Theor. Angew. Limnol. Verh.* **22:** 3170–3177.

HAIRSTON, N. G., JR., W. E. WALTON, AND K. T. LI. 1983. The causes and consequences of sex-specific mortality in a freshwater copepod. *Limnol. Oceanogr.* **28:** 935–947.

HOLTZER, T. O., J. R. BRADLEY, JR., AND R. L. RABB. 1976. Geographic and genetic variation in time required for emergence of diapausing *Heliothis zea. Ann. Entomol. Soc. Am.* **69:** 621–625.

HOY, M. A. 1977. Rapid response to selection for a nondiapausing gypsy moth. *Science* **196:** 1462–1463.

ISTOCK, C. A. 1981. Natural selection and life history variation: theory plus lessons from a mosquito. Pp. 113–128 in *Insect Life History Patterns: Habitat and Geographic Variation,* R. F. Denno and H. Dingle, eds. Springer, New York.

LUMME, J. 1982. Phenology and photoperiodic diapause in northern populations of *Drosophila.* Pp. 145–170 in *Evolution of Insect Migration and Diapause,* H. Dingle, ed. Springer, New York.

LUMME, J., AND A. OIKARINEN. 1977. The genetic basis of geographically variable photoperiodic diapause in *Drosophilia littoralis. Hereditas* **86:** 129–142.

MARCUS, N. 1980. Photoperiodic control of diapause in the marine calanoid copepod *Labidocera aestiva. Biol. Bull.* **159:** 311–318.

MARCUS, N. 1982. Photoperiodic and temperature regulation of diapause in *Labidocera aestiva* (Copepoda: Calanoida). *Biol. Bull.* **162:** 45–52.

MARCUS, N. 1984. Variation in the diapause response of *Labidocera aestiva* (Copepoda: Calanoida) from different latitudes and its importance in the evolutionary process. *Biol. Bull.* **166:** 127–139.

MASAKI, S. 1963. Adaptation to local climatic conditions in the Emma Field cricket (Orthoptera: Gryllidae). *Kontyu* **31:** 249–260.

MASAKI, S. 1967. Geographic variation and climatic adaptation in a field cricket (Orthoptera: Gryllidae). *Evolution* **21:** 725–741.

ROEN, U. 1957. Contributions to the biology of some Danish free living copepods. *Biol. Skr. Dan. Vid. Selsk.* **9:** no. 2. 101 pp.

SHOWERS, W. B., H. C. CHIANG, A. J. KEASTER, R. E. HILL, G. L. REED, A. N. SPARKS, AND G. J. MUSICK. 1975. Ecotypes of the European corn borer in North America. *Environ. Entomol.* **4:** 753–760.

SPINDLER, K. D. 1971. Dormanzauslösung und Dormanzcharacteristika beim Süsswassercopepoden *Cyclops vicinus. Zool. Jahrb. Abt. Allg. Zool. Physiol. Tiere* **76:** 139–151.

STROSS, R. G. 1969. Light and temperature requirements for diapause development and release in *Daphnia. Ecology* **47:** 368–374.

STROSS, R. G., AND J. C. HILL. 1965. Diapause induction in *Daphnia* requires two stimuli. *Science* **150:** 1462–1464.

TAUBER, C. A., AND M. J. TAUBER. 1981. Insect seasonal cycles: genetics and evolution. *Ann. Rev. Ecol. Syst.* **12:** 281–308.

TAUBER, M. J., AND C. A. TAUBER. 1970. Photoperiodic induction and termination of diapause in an insect: response to changing day lengths. *Science* **167:** 170.

TAUBER, M. J., C. A. TAUBER, AND S. MASAKI. 1985. *Seasonal Adaptations of Insects.* Oxford Univeristy Press. New York. 411 pp.

WALTON, W. E. 1985. Factors regulating the reproductive phenology of *Onychodiaptomus birgei* (Copepoda: Calanoida). *Limnol. Oceanogr.* **30:** 167–179.

WATSON, N. H., AND B. N. SMALLMAN. 1971. The role of photoperiod and temperature in the induction and termination of an arrested development in two species of freshwater cyclopoid copepods. *Can. J. Zool.* **49:** 855–862.

WILSON, M. S. 1959. Free-living Copepoda: Calanoida. Pp. 738–815 in *Freshwater Biology,* W. T. Edmondson, ed. Wiley, New York.